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Parrots of Oceania – a comparative study of extinction risk

George Olah [a], Jörn Theuerkauf [b], Andrew Legault [c], Roman Gula [b], John Stein[a], Stuart Butchart [d,e], Mark O'Brien [f] and Robert Heinsohn [a]

[a]Fenner School of Environment and Society, Australian National University, Canberra, Australia; [b]Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland; [c]Department of Conservation, New Zealand Government, Rangiora, New Zealand; [d]BirdLife International, Cambridge, UK; [e]Department of Zoology, University of Cambridge, Cambridge, UK; [f]BirdLife International, Pacific Partnership Secretariat, Suva, Fiji

ABSTRACT
Australia, New Zealand, New Guinea, Wallacea, and the islands of the Pacific Ocean collectively possess 42% of the world's parrot species, including half of all Critically Endangered species. We used comparative methods to review the factors related to extinction risk of 167 extant and 5 extinct parrot species from this region, subsequently referred to as 'Oceania'. We tested a range of ecological and socio-economic variables as predictors of extinction risk for parrots in the region while controlling for phylogeny. Parrot species were most likely to be threatened if they had small historical ranges, large bodies, or a high dependency on forest, or if they were endemic to a single country, or native to a country with high unemployment. Our analysis identifies invasive species as an especially severe threat to the parrots of Oceania. We present maps of parrot species' diversity and draw attention to regions of conservation concern. Our comparative analysis presents an important overview of the factors contributing to the decline of parrots in Oceania, and provides a strong basis for comparison with other parts of the world.

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Introduction

Parrots (Psittaciformes) originated on the Gondwanan supercontinent, likely during the Cretaceous period (Stidham 1998; Wright *et al.* 2008), and experienced a major radiation between 60 and 65 million years ago in Australasia (Cracraft 2001; Schweizer *et al.* 2010). There are currently 398 parrot species worldwide, but 112 (28%) are categorised as threatened according to the 2016 IUCN Red List (BirdLife International 2016; IUCN 2016). Among these, 55 are considered Vulnerable (VU), 39 are Endangered (EN), and 18 are Critically Endangered (CR). Of the remaining species, 60 are classified as Near Threatened (NT), and 226 are of Least Concern (LC) (BirdLife International 2016; IUCN 2016). Parrots carry a higher risk of extinction than most other birds (Butchart *et al.* 2004; Olah *et al.* 2016), which makes them an important group for identifying the factors underlying a wide and complex range of threatening processes.

Comparative analyses are useful tools in conservation biology because they help to prioritise conservation actions while taking phylogenetic factors into consideration (Fisher and Owens 2004). They have been used, for example, to predict which groups of species warrant additional conservation attention (Reed and Shine 2002), and to identify the underlying biological and anthropogenic factors associated with conservation issues (Bennett and Owens 1997). Olah *et al.* (2016) used comparative methods to assess the factors associated with higher extinction risk in parrots worldwide, and found that parrots were more likely to be threatened if they were endemic to a single country, or if they occurred in a country with a large urban population, or a high GDP. Parrots also faced a high risk of extinction if they had limited historical distributions, high dependency on forest, large bodies, or long life spans (Olah *et al.* 2016). Each of the studied regions had a distinct pattern of threats, suggesting that conservation solutions would differ on a regional basis (Olah *et al.* 2016). Recently, other authors have reviewed the specific issues affecting parrots in the Afrotropics (Martin *et al.* 2014), and in the Neotropics (Berkunsky *et al.* 2017). Forshaw and Knight (2017) also published a thorough overview of the world's extinct and threatened parrots.

Here, we focus on the factors affecting extinction risk in Oceania (i.e. Australia, New Zealand, New Guinea, Wallacea, and the Pacific Islands). This area contains 167 extant parrot species (42% of the world

CONTACT George Olah george.olah@anu.edu.au

total; Figure 1) from 48 genera (55% of 88 parrot genera), many of which are endemic to the region (Forshaw 2011; Forshaw and Knight 2017).

Oceania includes the large, developed countries of Australia and New Zealand, as well as a mixture of other developed and developing territories. New Guinea is one of the largest islands in the world, and is governed by the developing nations of Indonesia and Papua New Guinea. It is of high priority for parrot conservation, particularly due to the level of endemism, and the diversity of species found there. Indonesia also governs most of the islands in Wallacea (excluding Timor-Leste), which are rich in endemic species. For the purposes of this study, we treat the Pacific Islands as three discrete archipelagos: Micronesia, Melanesia (aside from New Guinea), and Polynesia (aside from New Zealand).

In this paper, we reviewed the parrot species of Oceania both qualitatively, by describing the different threats affecting them, and quantitatively, by using comparative models to identify the factors affecting extinction risk. We placed particular emphasis on Australia and the Pacific Islands, two subregions with sufficient parrot species and ecological data to investigate threatening processes in detail. We were also interested in assessing the impact that island endemism has on predisposing species to extinction, particularly considering that Oceania contains the highest rate of threatened endemic parrots in the world, and most extinct parrots occupied small islands (Olah *et al.* 2016). As many islands in the region are plagued by invasive species (Theuerkauf *et al.* 2010; Heinsohn *et al.* 2015), we predicted that this threat will have a large influence on the conservation status of parrots in Oceania. We reveal data deficiencies in the region, and highlight the species and locations most in need of focused conservation effort.

Methods

Database construction

We followed the taxonomy used by BirdLife International (2016) for non-passerines. Using BirdLife's data on species' distributions, we grouped the 167 parrot species from Oceania into five subregions (Figure 1): Australia (50 species), New Zealand (6), New Guinea (46), Wallacea (34), and the Pacific Islands (31). For the response variable of conservation status, we used the 2016 IUCN Red List (IUCN 2016) to assign a value of '1' to threatened species

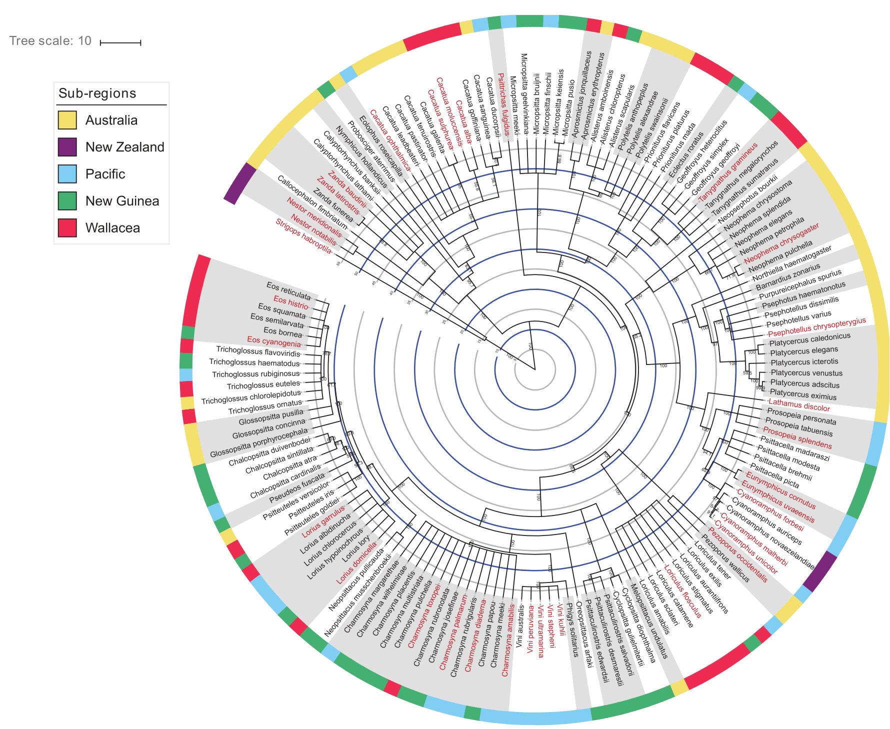

Figure 1. Consensus tree with 50% majority-rule of parrot species in Oceania (see also Provost *et al.* 2018). Coloured strips on the circumference represent the main subregions associated with each species: Australia (yellow), New Zealand (purple), the Pacific Islands (blue), New Guinea (green), and Wallacea (red). Grey shading is used to distinguish genera. Threatened species (Vulnerable, Endangered, and Critically Endangered) are labelled in red, and non-threatened species (Least Concern and Near Threatened) are labelled in black. Values on the nodes indicate the consensus support (%) based on 1000 trees from birdtree.org. The phylogenetic tree is available in colour at http://itol.embl.de/shared/olahgy.

(VU/EN/CR), and a value of '0' to non-threatened species (LC/NT). We divided the large number of explanatory variables into four groups: (A) geographical and distributional attributes of each species, (B) biological, ecological and life history variables, (C) type of utilisation by humans, and (D) socio-economic and demographic attributes of the countries where the species occur. For detailed descriptions, sources of data, and values of each variable see Table 1. We used ArcGIS 10.41 to calculate the extent, and average latitude, of the distribution of each species. We calculated the size of each species' historical range from species range maps (BirdLife International and Handbook of the Birds of the World 2016). We mapped historical distributions using the same sources as for contemporary distributions, but added in areas where the species was recorded before 1980, yet either had no recent survey records, lacked suitable habitat, or were deemed inappropriate based on expert opinion (BirdLife International and Handbook of the Birds of the World 2016). Historical range size and body size were normalised using natural logarithms.

Statistical modelling

We fitted a logistic regression model (correlating explanatory variables to the binary response variable) using the 'GLM' function in R statistics (R Core Team 2011). We carried out analyses separately for each group (A–D) of explanatory variables. First, we performed a likelihood ratio test (LRT) on each group, including all possible variables. We used this to select the best model with only the statistically significant variables. Then, we ran the model with the chosen variables to calculate *P* values for each of the included variables. We generated one model for all of Oceania (167 species), and two additional models for Australia and the Pacific Islands, as these regions contain sufficient species and information to assess local threats in more detail. For the Australian analysis, we used the *Environment Protection and Biodiversity Conservation Act* (EPBC 2016) to determine conservation status. We conducted the analysis on 54 native Australian parrots, including four species whose main range is located elsewhere: Double-eyed Fig-parrot (*Cyclopsitta diophthalma*), Eclectus Parrot (*Eclectus roratus*), Red-cheeked Parrot (*Geoffroyus geoffroyi*), and Palm Cockatoo (*Probosciger aterrimus*). We carried out a separate analysis on the 31 parrot species native to the Pacific Islands.

Phylogenetic control and tree

We generated 1000 possible phylogenetic trees of parrots, and used branch lengths and nodes to portray phylogenetic relatedness among species (Jetz *et al.* 2014; see also Provost *et al.* 2018). For each phylogeny, we ran a phylogenetic generalised least squares (PGLS) regression using the 'caper' package in R (Freckleton *et al.* 2002). The explanatory and response variables were the same as those used in the regression models. For each explanatory variable, we report the modified *P* value accounting for phylogenetic relatedness. For each model, we report a variable (lambda transformation) that improves the fit of the phylogenetic data. Greater lambda values indicate that the relationship between response and explanatory variables correlates with the phylogeny, and that the values of the explanatory variables are more similar for closely related species. We also include the mean and standard deviation of lambda, calculated from 1000 phylogenetic hypotheses for each model.

We created a 50% majority-rule consensus tree with Geneious R6 (Kearse *et al.* 2012), using 1000 trees downloaded from birdtree.org. For each node, we report the clade credibility value (consensus support of the given node, as a percentage). Only 151 species were included in the tree, as 16 species were missing from the birdtree.org dataset. We generated Figure 1 using iTOL v3 (Letunic and Bork 2016).

Heat maps and analysis of threats

We estimated the area of each species' range using digital distribution maps (BirdLife International and Handbook of the Birds of the World 2016). These ranges were derived from a variety of sources (for detailed description see Buchanan *et al.* 2011). We used the union function in ArcGIS 10.4.1 to generate heat maps of species richness by overlaying the range of each parrot species in Oceania. The number of species in each overlapping polygon were then summed, excluding Extinct and non-native species. We also generated a heat map showing where the most threatened species occur, following the 2016 IUCN Red List categories (VU/EN/CR).

We analysed the threats affecting parrots using the same procedures as Olah *et al.* (2016). First, we estimated impact scores based on the timing, scope and severity of threats listed by BirdLife International (2016), then we pooled the medium- and high-impact scores. For all of Oceania, we determined how many species were impacted by each threat, and to what extent. We also estimated how many parrot species were impacted by the threats in each subregion. As few of the extinct parrots in Oceania were studied in detail, we pooled data from both Extinct and Critically Endangered species, then compared their collective traits with those of extant species using means and 95% confidence intervals in R (R Core Team 2011).

Table 1. Explanatory variables used in the statistical models. The four groups of variables represent (A) geographical and distributional attributes of each species, (B) biological, ecological and life history variables, (C) type of utilisation by humans, and (D) socio-economic and demographic attributes of the countries where the species occur

Group	Variable name	Description	Values	Source of data
A	Average Latitude	Absolute value of the average of northern and southern limits of a species range	Decimal degree of latitude	BirdLife International and Handbook of the Birds of the World (2016)
	Historical Distribution Size[a]	Previous extent of the species' range based on modern and historical records	km^2	BirdLife International and Handbook of the Birds of the World (2016)
	Mean Altitude	Mean elevation of the species range	m	BirdLife International (2016)
	Subregion	Distribution of the species (categorical variable)	(1) Australia, (2) New Zealand, (3) Pacific Islands, (4) New Guinea, (5) Wallacea	Olson *et al.* (2001)
	Island Endemism	If the species is endemic to islands smaller than 110 000 km^2 (this excludes large islands, such as New Guinea, Borneo, Sumatra, Celebes/Sulawesi, New Zealand, Java)	Yes/no	BirdLife International (2016)
B	Body Size[a]	Length of the species	cm	Forshaw (2011)
	Migratory Status	The stage of the migratory status of the species (categorical variable)	(0) Not a Migrant, (1) Nomadic, (2) Altitudinal Migrant, (3) Full Migrant	BirdLife International (2016)
	Main Diet	The main food items consumed by the species (categorical variable)	(1) Frugivore (fruits, vegetable matter, leaves, fungi, lichens), (2) Granivore (grass seeds), (3) Nectarivore (nectar, pollen, flowers), (4) Tree seeds (hard seeds, acorns, nuts, cone seeds), (5) Specialist	Juniper and Parr (2003)
	Social Flocking	Flock size in the non-breeding season (categorical variable)	(0) No flocks (alone or pairs), (1) Small flocks (up to 20), (2) Large flocks (more than 20)	Arndt (2007); Forshaw (2011)
	Colony Nesting	If the species nests in colonies	Yes/no	Forshaw (2011)
	Nesting Tree Type	The main nest type used by the species (categorical variable)	(1) Hardwood trees and their branches; (2) Palm trees; (3) Other nest types (e.g. termite mounds, epiphytes, moss, burrows, grass, etc.)	Juniper and Parr (2003); Forshaw (2011)
	Forest Dependency	Scored from published and unpublished information on the ecology of each species (categorical variable)	(0) Non-forest, (1) Low, (2) Medium, (3) High	BirdLife International (2016)
	Generation Time	Mean generation length	Years	BirdLife International (2016)
C	Captive Breeding	If the species breeds regularly in captivity	Yes/no	Arndt (2007)
	Used for Pets	Pets are defined as those species recorded as being kept in captivity, either as personal pets or for display in zoos, collections etc.	Yes/no	BirdLife International (2016)
	Used for Food	If the species is used for food	Yes/no	BirdLife International (2016)
	Used for Accessories	If the species is used for making accessories	Yes/no	BirdLife International (2016)
	Used for Sport	If the species is used for sport purposes	Yes/no	BirdLife International (2016)

(*Continued*)

Table 1. (Continued).

Group	Variable name	Description	Values	Source of data
D	Single Country Endemic	If the species is endemic to one country	Yes/no	BirdLife International (2016)
	Per capita GDP	Gross domestic product based on purchasing-power-parity (PPP) per capita	Amount in US$	CIA (2013); IMF (2013)
	Industrial Production Growth Rate	Industrial production growth rate of countries where species is extant	Mean percentage	CIA (2013)
	Unemployment Rate	Unemployment rate of countries where species is extant	Mean percentage	CIA (2013), IMF (2013)
	Human Population Density	Mean population density of countries where species is extant	Number of people/1000 ha	CIA (2013); FAOSTAT (2013); IMF (2013)
	Urban Population	Human population living in urban areas of countries where species is extant	Mean percentage	FAOSTAT (2013)
	Human Population Growth Rate	Human population growth rate of countries where species is extant	Mean percentage	CIA (2013)
	Agricultural Area	Agricultural area of countries where species is extant	Mean percentage	FAOSTAT (2013)

[a] $\log_e$ transformed variables.

Results and discussion

Oceania possesses 42% of the world's parrot species, including half (9 out of 18) of those classified as Critically Endangered. It was a focal point for the early diversification of parrots and includes many early lineages of the psittaciform phylogeny (Figure 1; Wright *et al.* 2008; Schweizer *et al.* 2010; Schweizer *et al.* 2011). The region accounts for much of the phylogenetic diversity of this charismatic order of birds. However, 37 of the 167 extant parrot species in Oceania are currently threatened with extinction, and the specific conservation requirements of many species remain poorly understood. We attempted to address some of these knowledge gaps by extracting information from large, up-to-date international datasets (BirdLife International 2016; IUCN 2016). While we acknowledge that there are shortcomings and inaccuracies in such databases (see below), they are invaluable for broad-scale analyses of extinction risk, and useful for identifying data deficiencies. Our analysis identifies the major threats impacting parrots in Oceania, and the species and areas most urgently in need of conservation.

In Oceania, 5 parrot species are considered Extinct, 9 are Critically Endangered, 12 are Endangered, 16 are Vulnerable, 19 are Near Threatened, and 111 are categorised as Least Concern. New Zealand has the highest percentage of threatened parrot species (67%), followed by the Pacific (42%), Wallacea (29%), Australia (14%), and New Guinea (7%; Figures 2 and 3).

Historical range size and single-country endemism are important predictors of extinction risk for the parrots of Oceania (Table 2). Species with naturally small ranges appear to be more prone to threats than others, possibly as a result of limited habitat availability and lower dispersal capacity. Although island endemism was not a predictor of conservation status, its importance may have been overshadowed by the inclusion of other variables, such as historical range size and endemism to a single country.

In Oceania, the probability of extinction was higher for larger parrot species, and those with stronger dependence on forest (Table 2). Larger body size is correlated with lower reproductive outputs, which may hinder population recovery after disturbance (Cardillo *et al.* 2005). Larger animals are also at greater risk of being hunted (Cowlishaw and Dunbar 2000). Like other parts of the world, parrots in Oceania rely on trees for nest cavities and food (Snyder *et al.* 2000), and it is this dependency that makes them so vulnerable to forest loss and degradation.

Throughout Oceania, parrots were more likely to be threatened in less-developed countries with high unemployment rates (Table 2). These countries often have higher rates of poaching, causing a high degree of pressure on parrot populations, particularly where there is a shortage of paid work (Wright *et al.* 2001; Barré *et al.* 2010). There is little published information about the extent of trapping in Oceania, but the parrot trade is generally more active in less-developed countries (Pain *et al.* 2006). Parrot species that are kept as pets tend to be less threatened in Oceania (Table 2), and elsewhere in the world (Olah *et al.* 2016). However, this might be because common species are more likely to be kept as pets (Butchart 2008;

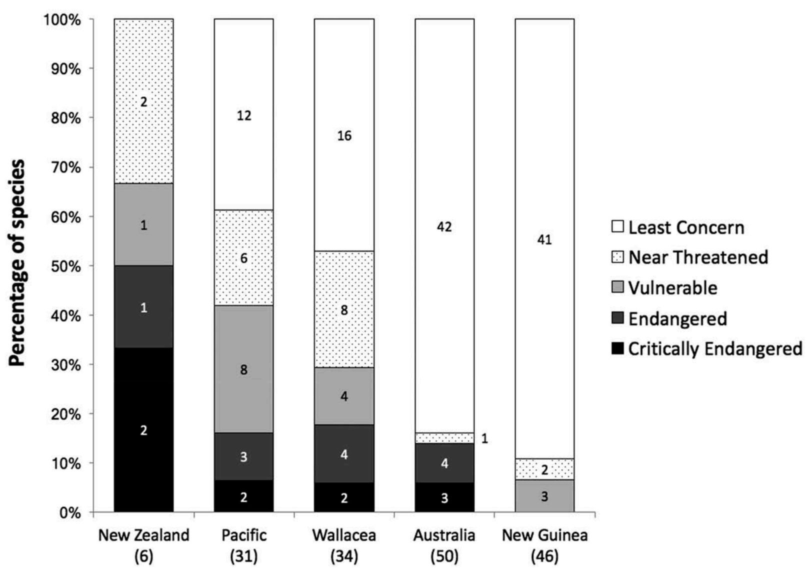

Figure 2. Extinction risk of parrot species in Oceania, derived from BirdLife International's assessments for the 2016 IUCN Red List. Columns are broken into the percentage of species per category in each subregion. Digits represent the number of species.

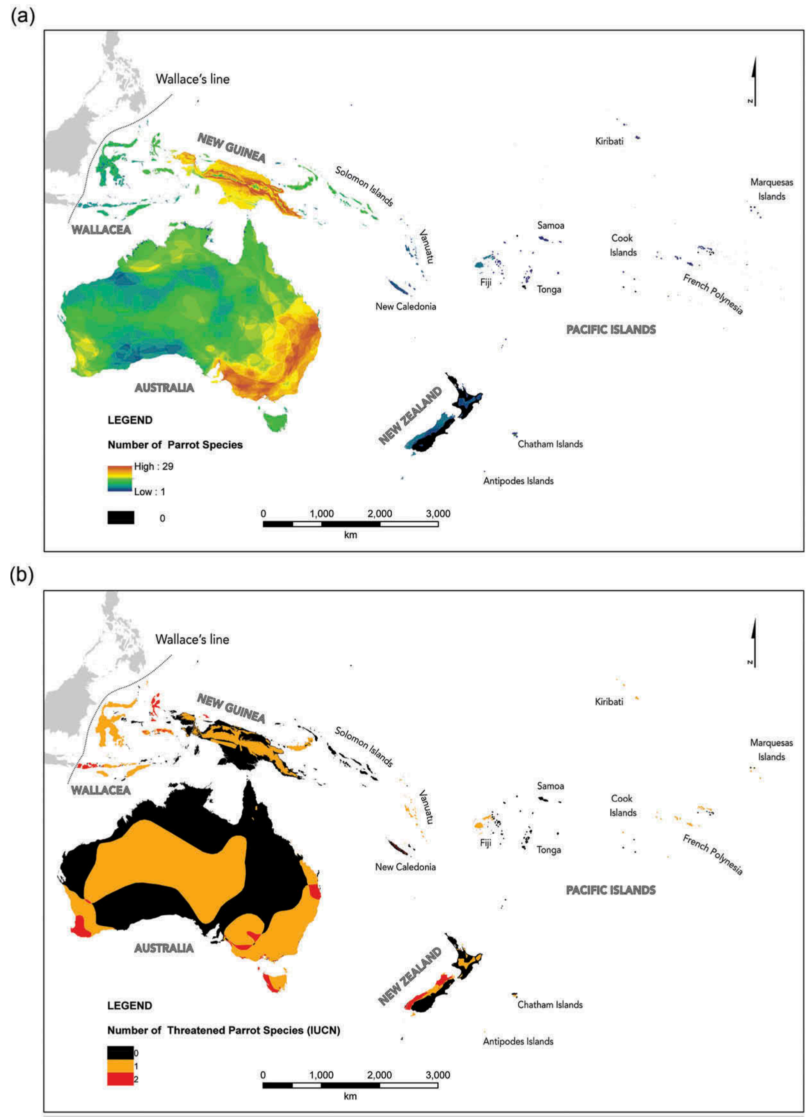

Figure 3. Heat maps of parrot species diversity and extinction risk in Oceania. (A) Species richness map of parrots in Oceania, generated by overlaying the distribution maps of parrot species in the region. (B) Richness of threatened (Vulnerable, Endangered, and Critically Endangered) parrot species in Oceania, generated by overlaying the current distribution maps of threatened parrot species in the region. Colour codes indicate the number of parrot species.

Pires 2012; Vall-Llosera and Cassey 2017). Although latitude is not a significant factor in explaining extinction risk among parrots globally (Olah *et al.* 2016), it appears to be a significant factor in Oceania, with higher-latitude species more likely to be threatened (Table 2). This is possibly driven by the relatively high proportion of threatened parrots in Tasmania and New Zealand (Figure 3(B)), which have suffered from the introduction of non-native predators (Dilks *et al.* 2003; Heinsohn *et al.* 2015).

Parrots in Oceania were threatened mainly by logging (23% of species), agriculture (18%), hunting and trapping (17%), invasive species (16%), fire and fire-suppression, outside of natural range or frequency (4.2%), residential and commercial development (4%), energy production and mining (4%), and climate change and severe weather (4%; Figure 4). On a global scale, agriculture has the largest impact on the extinction risk of parrots (Olah *et al.* 2016), but in Oceania parrots were mostly threatened by logging (i.e. harvesting trees for timber, fibre, or fuel), and for many species this impact is considerable (Figure 4(A)). The conversion of native forest to tree plantations (e.g. oil palm plantations in Indonesia) is known to have an adverse effect on native biodiversity (Koh and Wilcove 2008), and also reduces habitat for most forest-dwelling parrots in the region. Invasive species threaten a greater proportion of parrots in Oceania than elsewhere in the world (Olah *et al.*

Table 2. The statistical significance of four groups of variables as predictors of the likelihood of parrot species in Oceania being threatened (VU/EN/CR). Results of the binomial logistic regression are provided with the likelihood ratio test (LRT), degree of freedom (df), and chi-square *p* values (P_{chi}). Results from the phylogenetic generalised least squares (PGLS) model are provided as the means of the estimate with their standard deviation (SD) in parentheses, *p* values (P_{PGLS}), and lambda (λ) values for each PGLS model with SD in parentheses

Group[a]	Variable	LRT	df	P_{chi}	PGLS estimate (SD)	P_{PGLS}	λ (SD)
A	Average Latitude	9.19	1	0.004	−0.009 (0.001)	<0.001	0.039 (0.103)
	Historical Range Size ($\log_e$)	10.15	1	<0.001	−0.089 (0.001)	<0.001	
	Mean Altitude	4.47	1	0.101			
B	Body Size ($\log_e$)	4.77	1	0.018	0.192 (0.008)	0.037	0.363 (0.167)
	Forest Dependency	5.44	4	0.002	0.136 (0.002)	<0.001	
C	Used for Pets	7.02	1	0.026	−0.287 (0.009)	0.009	0.534 (0.063)
	Used for Sport	5.56	1	0.987			
D	Single-country Endemic	12.36	1	0.004	0.212 (0.006)	0.002	0.412 (0.109)
	Unemployment rate	3.90	1	0.037	0.028 (0.001)	0.008	

[a] A: geography and distribution, B: biology, C: type of utilisation by humans, D: socio-economy and demography.

2016). Of the other threats facing parrots in Oceania, only logging, agriculture, and poaching have negative impacts of comparable magnitude (Figure 4(A)).

Parrots of Australia

Australia, including its offshore islands, has 54 species of parrots, of which 15 are currently listed as threatened (EPBC 2016). In our analysis of this subregion, we found that Australian parrots were more likely to be threatened if they had small historical ranges (LRT = 2.82, df = 1, P_{PGLS} = 0.001). On average, the historical range of threatened parrot species in Australia was 721 000 km^2 (SD = 931 000), compared to 1 673 000 km^2 (SD = 1 851 000) for non-threatened species. Coxen's Fig-parrots (*Cyclopsitta coxeni*) and Palm Cockatoos (*Probosciger aterrimus macgillivrayi*) provide examples of threatened rainforest taxa with relatively small ranges that are severely affected by deforestation and habitat degradation (Coxen's Fig-parrot Recovery Team 2001; Heinsohn *et al.* 2003, 2009; Murphy *et al.* 2003; Russell-Smith *et al.* 2004).

We also found that larger Australian parrots were more likely to be threatened by extinction than smaller species (LRT = 4.95, df = 1, P_{PGLS} = 0.005). Threatened Australian parrots had a mean body size of 40 cm (SD = 16), compared to 29 cm (SD = 10) for non-threatened species. Palm Cockatoos, along with four other threatened black-cockatoo species (*Calyptorhynchus* spp. and *Zanda* spp.), exemplify the conservation status of large-bodied parrots in Australia. The south-western subspecies of the Red-tailed Black-Cockatoo (*Calyptorhynchus banksii naso*) is threatened by the loss of nest hollows from mining (Chapman 2007), the transformation of forest into agricultural land (Abbott 1998), and also from competition for hollows with species such as the European Honey Bee (*Apis mellifera*) (Johnstone and Cassarchis 2004). The south-eastern subspecies (*C. b. graptogyne*) is threatened due to major clearing of its woodland habitat (Maron 2005). Long-billed Black-cockatoos (*Zanda baudinii*) and Carnaby's Black-cockatoos (*Z. latirostris*) have suffered from habitat loss as well. The Kangaroo Island subspecies of Glossy Black-Cockatoo (*Calyptorhynchus lathami halmaturinus*) has also suffered major population declines, mainly due to increased predation by Common Brushtail Possums (*Trichosurus vulpecula*) and forest clearing (Garnett *et al.* 1999; Lee *et al.* 2013).

In contrast with the trends observed in Oceania as a whole, Australian parrots were most likely to be threatened by invasive species (18%), followed by agriculture (12%), and hunting and trapping (10%; Figure 4(B)). For instance, the migratory Swift Parrot (*Lathamus discolor*) has suffered a severe decline in Tasmania due to habitat loss caused by residential and industrial development, and because of predation by introduced Sugar Gliders (*Petaurus breviceps*) (Heinsohn *et al.* 2015). Another migratory species from Tasmania, the Orange-bellied Parrot (*Neophema chrysogaster*), is currently on the brink of extinction in the wild due to degradation of wintering habitat by grazing, agriculture, urban development, and predation by introduced foxes and cats in their breeding range (DELWP 2016). Reasons for the decline of the recently rediscovered, cryptic Night Parrot (*Pezoporus occidentalis*) are unknown, but are likely to include predation by cats and foxes, loss of mature spinifex habitat by altered fire regimes, and habitat degradation by introduced rabbits and camels (Whitlock 1924; Blyth 1997; Pyke and Ehrlich 2014; Murphy *et al.* 2018).

Many Australian parrot species (e.g. black-cockatoos) are threatened by the transformation of their preferred habitat into agriculture. This threat was the second highest in Australia (Figure 4(B)), having impacts on 12% of parrot species. The third highest threat was trapping, impacting 10% of the Australian parrot species. Although trapping for the international trade is kept to a minimum through strict

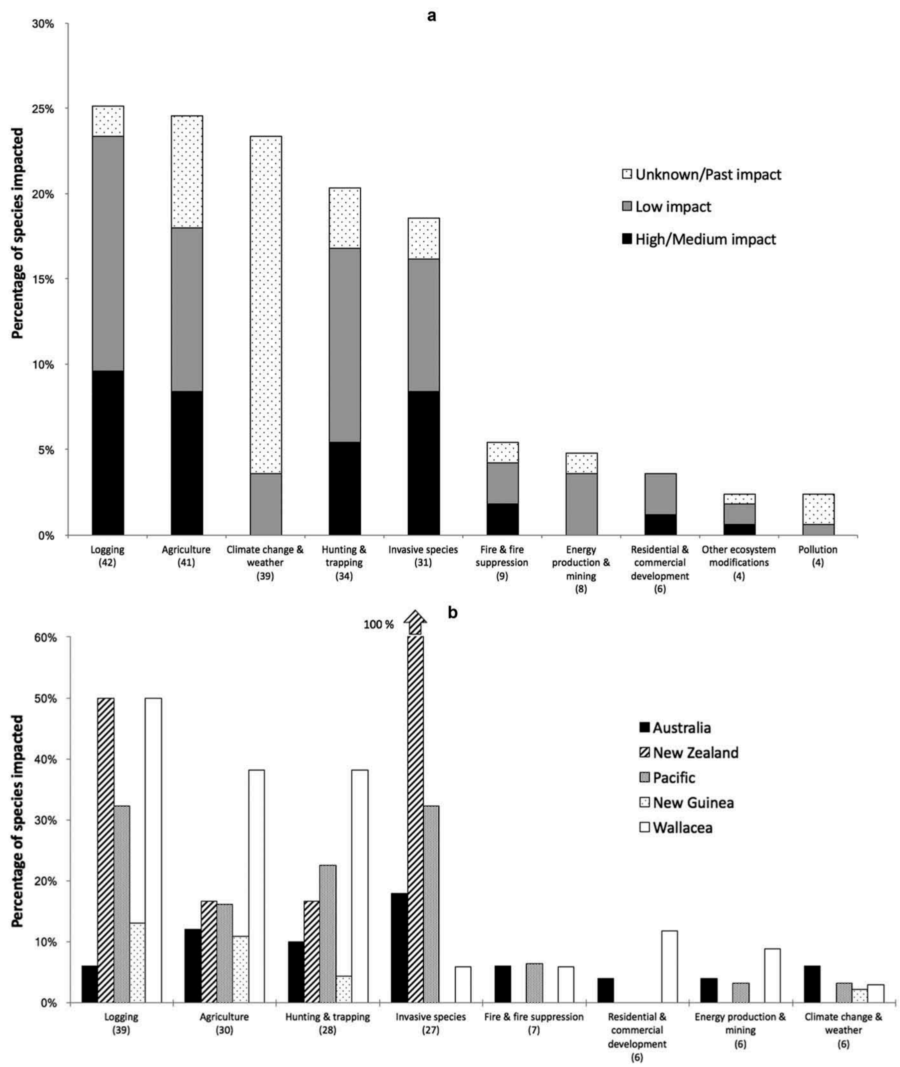

Figure 4. Percentage of parrot species impacted by different threats in (A) Oceania, and (B) each subregion of Oceania. Threat impact is extracted from BirdLife International (2016), calculated from scores for timing, scope and severity of threats. Only threats impacting more than five species were plotted. The number of species impacted by each threat is given in parentheses.

biosecurity frameworks (Vall-Llosera and Cassey 2017), this threat class also includes persecution for pest control, a more common issue affecting Australian parrots (Ainsworth *et al.* 2016).

Parrots of New Zealand

As part of the first major landmass to split from Gondwana, New Zealand is home to an ancient parrot family (Strigopidae), which includes the Kakapo (*Strigops habroptila*), Kea (*Nestor notabilis*) and Kaka (*Nestor meridionalis*; Figure 1), and is a sister clade to all other parrots (Schweizer *et al.* 2011). The remainder of New Zealand's parrots are *Cyanoramphus* species, including the Yellow-crowned Parakeet (*Cyanoramphus auriceps*), Red-crowned Parakeet (*Cyanoramphus novaezelandiae*), and Orange-fronted Parakeet (*Cyanoramphus malherbi*). The Chatham Islands and Antipodes Islands also possess several *Cyanoramphus* parakeets, but these have been treated here as Pacific Islands, on account of their isolation.

While there are too few parrot species in the region for statistical analysis, some generalisations can be made. Of the six species assessed, four were threatened with extinction, and all were impacted by invasive species (Figure 4(B)). Half of the species were impacted by logging (Figure 4(B)), but this was mostly in the past, or localised.

It is worth noting that several of the mammalian predators introduced to New Zealand are absent from other islands in the Pacific, which may explain why New Zealand has suffered such a disproportionate loss of native species.

Stoats (*Mustela erminea*) and Common Brushtail Possums have been implicated in the decline of a range of endemic birds, including the Yellow-crowned Parakeet (Elliott *et al.* 1996), Red-crowned Parakeet (Greene 2003), and Orange-fronted Parakeet (Kearvell 2002), as well as the larger parrots, such as Kea (Elliott and Kemp 2004), Kaka (Dilks *et al.* 2003; Moorhouse *et al.* 2003), and Kakapo (Clout and Merton 1998). Rats also pose a serious threat to New Zealand's parrots. For example, less than 4 years after the establishment of Black Rats (*Rattus rattus*) on Big South Cape Island, populations of Red-crowned Parakeets and Yellow-crowned Parakeets were experiencing major declines (Atkinson 1985; Ortiz-Catedral and Brunton 2010). Rodents and rabbits are also capable of sustaining abnormally high densities of predators, especially cats, which have the potential to decimate populations of native species (Johnstone 1985).

In New Zealand, the impact of predators is exacerbated by a phenomenon known as 'masting'. The southern beech forests (*Fuscospora* spp.) provide extensive habitat for parrots, and in 'mast' years they produce copious quantities of seed (Fitzgerald *et al.* 2004). This presents an opportunity to breed, not only for parakeets but also for mice, rats, and subsequently, Stoats and Weasels (*Mustela nivalis*). When the seed runs out, rodent numbers crash, and mustelids target native birds instead (Studholme 2000; Fitzgerald *et al.* 2004; McQueen and Lawrence 2008).

The Orange-fronted Parakeet is currently facing extinction in the wild (Robertson *et al.* 2013), largely as a result of these predator plagues (O'Donnell 1996; Kearvell *et al.* 2002). The decline of Yellow-crowned Parakeets has not been as dramatic, perhaps because they forage less frequently in the understorey (Elliott *et al.* 1996; Kearvell 2002). In contrast, Red-crowned Parakeets have been extirpated from most parts of the mainland (Taylor 1985), presumably due to their tendency to forage and nest on the ground (Greene 1998). The decline of the Red-crowned Parakeet was probably accelerated by an increase in browsers, especially deer, which generate a more open hunting environment for cats, and other predators (Kearvell 2002).

Several other suggestions have been proposed to account for the decline of Orange-fronted Parakeets, including competition with Yellow-crowned Parakeets for food and nesting hollows, competition with introduced finches (*Carduelis* spp.) for seed, and competition with invasive wasps (*Vespula* spp.) for invertebrates (Kearvell *et al.* 2002). Given that a considerable proportion of parakeet nestlings die of starvation in the wild (Greene 2003; Ortiz-Catedral *et al.* 2013), it is possible that competition could influence reproductive output, particularly if competitors are sufficiently abundant to restrict food availability.

While Kaka are subject to competition from wasps and possums (Beggs and Wilson 1991; Wilson *et al.* 1998), their main limiting factor appears to be predation, primarily from Stoats and possums, which prey upon eggs, chicks, and nesting females (Wilson *et al.* 1998; Moorhouse *et al.* 2003).

Kea populations have also declined as a result of nest predation, most likely by Stoats and possums (Elliott and Kemp 2004). Although Kea nest in cavities on the ground, their tendency to select very steep nest sites near the bush-line probably reduces their accessibility to predators (Elliott and Kemp 1999, 2004).

Kakapo are particularly vulnerable to introduced mammals, especially Stoats and cats (Clout and Craig 1995; Powlesland *et al.* 2006b). This large, flightless parrot would likely be extinct if the last known individuals had not been translocated to offshore islands that are free of mammalian predators (Clout 2006). The last natural population was discovered on Stewart Island, one of the few sites in New Zealand that has not been invaded by Stoats (Powlesland *et al.* 2006b).

Parrots of the Pacific Islands

There are 31 extant parrot species in the Pacific Islands (Figure 1), but nearly half (47%) are threatened with extinction (Figure 2). Recent population estimates suggest that the New Caledonian Parakeet is also threatened with extinction (Legault *et al.* 2013). However, it was included here as a subspecies of the Near Threatened Red-crowned Parakeet (*C. novaezelandiae*), following del Hoyo and Collar (2014). Nevertheless, genetic evidence (Boon *et al.* 2001), biogeographical discrepancies, and differences in calls and behaviour (Theuerkauf *et al.* 2009) suggest that the taxon should be treated as a full species.

In our analysis of the parrots from this subregion, we found that species were more likely to be threatened if they occurred at higher latitudes (i.e. further south from the equator; LRT = 4.37, df = 1, P_{PGLS} = 0.001). On average, threatened species in the Pacific Islands had ranges with a mean latitude of 21° S (SD = 13), while non-threatened species had ranges with a mean latitude of 8° S (SD = 6). This is largely attributed to the inclusion of the Chatham Parakeet (*Cyanoramphus forbesi*) from the Chatham Islands (44.0° S), and the Antipodes Parakeet (*Cyanoramphus unicolor*) from the Antipodes Islands (49.7° S), both of which are classified as Vulnerable. Although these two southern archipelagos are territories of New Zealand, we treated them as Pacific Islands for this study.

We also found that parrot species in more urbanised countries within this subregion were more likely to be threatened (LRT = 8.96, df = 1, $P_{PGLS} = 0.002$). The loss of habitat associated with urbanisation is often more permanent and destructive than other types of land use (McKinney 2002), and it tends to have a disproportionate impact on small islands. Urbanisation is also linked to other forms of economic development and activity, which can pose additional risks to parrots (Olah *et al*. 2016).

Invasive species were the most frequently reported threats (32%) to parrots in the Pacific Islands (Figure 4(B)). In this subregion, cats and Black Rats are the most detrimental introduced predators. These species are known to prey occasionally upon parrots in New Caledonia (Gula *et al*. 2010), and they have probably influenced the distribution of parrots in some forested areas (Legault *et al*. 2013). Interestingly, rainforests on oligotrophic soils appear to provide some refuge for New Caledonian Parakeets and Horned Parakeets (*Eunymphicus cornutus*) (Legault *et al*. 2011), possibly because rat density is lower there (Rouys and Theuerkauf 2003). Small parrots, particularly those belonging to the genus *Charmosyna* or *Vini*, appear to be particularly vulnerable to Black Rats (Rinke *et al*. 1992; Ziembicki 2003). Even populations of relatively widespread species, such as the Blue-crowned Lorikeet (*Vini australis*), may not be secure. While many island nations have biosecurity measures in place to prevent the establishment of rats, and other alien pests, introductions still occur (Theuerkauf *et al*. 2010). As exemplified with the Ultramarine Lorikeet (*Vini ultramarina*), declines associated with such introductions can be swift (Ziembicki 2003). Rats can also have an indirect effect on parrots by acting as a food source for introduced predators such as cats (Atkinson 1985). Predators take advantage of the increased availability of prey, and as their populations expand, the pressure on native species escalates. For example, parakeets coexisted with cats for over 60 years on Macquarie Island, yet the release of rabbits in 1879 provided such an abundant food source that, in little more than a decade, cats had multiplied and spread across the island, and the endemic Macquarie Island Parakeet (*Cyanoramphus novaezelandiae erythrotis*) had been driven to extinction (Taylor 1979).

The clearing of land for agriculture has had major impacts in the past, and continues to affect 16% of parrot species on Pacific Islands (Figure 4(B)). For example, much of the fertile, lowland terrain has been burnt or cleared in New Caledonia, and elsewhere in the Pacific. Before European settlement, Melanesians and Polynesians used fire to establish and maintain an open landscape, and to improve the productivity of crops. In the 19th century, European colonisers subsequently removed vast tracts of native vegetation for agriculture, livestock and timber (Bouchet *et al*. 1995; Stevenson 2004; McWethy *et al*. 2010). Today, logging for timber poses a serious threat to parrots in the Pacific Islands, with 32% of species being impacted (Figure 4(B)). In New Caledonia, it is likely that the absence of parakeets in lowland areas is largely due to forest loss, rather than altitudinal preferences (Legault *et al*. 2011, 2013). Deforestation in lowland areas has undoubtedly displaced many species, and is likely to have led to the extinction of others. It is possible, for example, that the New Caledonian Lorikeet (*Charmosyna diadema*) was seasonally dependent upon the sclerophyll forests along the west coast of New Caledonia (Ekstrom *et al*. 2002), which have all but disappeared (Bouchet *et al*. 1995; Veillon *et al*. 1999).

Trapping threatens 23% of the parrot species native to the Pacific Islands (Figure 4(B)). The extent of the parrot trade on most Pacific Islands is largely unknown, and needs further investigation. However, in the Solomon Islands, falsified claims about the origin of wild-caught parrots have led to an alarming number of parrots being exported (Shepherd *et al*. 2012). Although invasive species and habitat loss remain the main threats to parrots in the Pacific Islands, disease is of growing concern, particularly with the rise of travel and tourism, which facilitate the spread of infectious agents around the world (Ortiz-Catedral *et al*. 2009; Jackson *et al*. 2014). Climate change also has the potential to place parrot species at risk by accelerating the loss and fragmentation of suitable habitat (Legault *et al*. 2013). Insular species are particularly vulnerable, not only from shifting climate envelopes but also from climate-induced changes in sea level (Weeks *et al*. 2016).

Among the parrots of the Pacific Islands, the New Caledonian species have been most intensively studied (Robinet *et al*. 2003; Theuerkauf *et al*. 2009; Legault *et al*. 2013). For French Polynesia, there are a number of publications on the conservation of parrots (Graves 1992; Kuehler *et al*. 1997; Lieberman *et al*. 1997; Ziembicki 2003; Ziembicki and Raust 2004), but few concerning their biology (Gerischer and Walther 2003). There is some information available on the parrots of Tonga (Rinke 1989; Rinke *et al*. 1992; Butler and O'Brien 2015), Solomon Islands (Webb 1992; Kratter *et al*. 2001; Danielsen *et al*. 2010; Read 2013), and Fiji (Masibalavu and Dutson 2006; Jackson and Jit 2007; Franklin and Steadman 2011; Morley and Winder 2013). However, there are limited data for the parrots on most other islands, such as Kiribati (Watling 2010), Niue (Powlesland *et al.* 2006a; Butler *et al.* 2012), Vanuatu (Kratter *et al.* 2006), and Cook Islands (Steadman 1991; Wilson 1993).

Parrots of Wallacea and New Guinea

The islands of Wallacea are inhabited by 34 extant parrot species (Figure 1), of which 29% are threatened (mostly in the Moluccas and the Lesser Sundas; see Figure 2, 3(B)). Parrots in this subregion are impacted by the same major threats affecting Oceania as a whole: logging (50%), agriculture (38%), and hunting and trapping (38%; Figure 4(B)). Lowland forests on the islands of Wallacea, which provide the most important habitat for threatened parrots, face continued threat from deforestation (Marsden and Fielding 1999). For example, the Blue-fronted Lorikeet (*Charmosyna toxopei*) persists in low numbers on a single island (Buru) with rapidly shrinking habitat (BirdLife International 2016).

In other regions, such as the Neotropics, parrot trapping is mostly an opportunistic activity undertaken by the inhabitants of poor villages (Pires and Clarke 2011). However, in Indonesia, it can be a profession, and certain villages specialise in bird trapping (Jepson *et al.* 2001; Butchart *et al.* 2010). The Yellow-crested Cockatoo (*Cacatua sulphurea*) is now Critically Endangered as a result of unsustainable trapping for the pet trade (Collar and Marsden 2014; BirdLife International 2016), and e.g. only a few individuals of the subspecies *C. s. abbotti* have survived on one island belonging to the Masalembu archipelago (Metz *et al.* 2009; Nandika and Agustina 2012).

New Guinea is similarly rich in parrot diversity, with 46 native species (Figure 1), though only 7% are considered threatened (Figure 2). Most of the threatened species inhabit the satellite islands of New Guinea, with the exception of Pesquet's Parrot (*Psittrichas fulgidus*), which lives on the mainland (Figure 3(B)). Although there are surprisingly few threatened parrot species in New Guinea, many are very poorly known (Marsden *et al.* 2001; Marsden and Pilgrim 2003; Marsden and Symes 2006), and further information may lead to revisions of their Red List status.

Extinct and Critically Endangered parrots in Oceania

A total of five parrot species are known to have become extinct in Oceania since the 16th century (IUCN 2016). One of these extinct species was native to Australia, and the other four species occurred in the Pacific Islands (Table 3). Of the extant species, nine are classified as Critically Endangered, including three in Australia, two in New Zealand, two in the Pacific Islands, and two in Wallacea (Table 3). After pooling the Extinct and Critically Endangered parrots, we noted that all but one species (93%) were endemic to a single country. In contrast, only 60% of the species in lower-risk categories were endemic to a single country. The mean historical range of Extinct and Critically Endangered species was smaller (129 000 km^2 ± 128 000 CI 95%, N = 14) than that of less-threatened species

Table 3. List of Extinct (EX) and Critically Endangered (CR) parrot species in Oceania, including scientific and common names, 2016 IUCN Red List category, subregion of occurrence, distribution, average latitude of range (degrees), current size of their mapped range (km^2), and estimated population size (number of mature individuals)

Scientific name	Common name	Red List category	Subregion	Distribution	Latitude (°)	Range (km^2)	Population size
Psephotellus pulcherrimus	Paradise Parrot	EX	Australia	Eastern Australia	−26.5	NA	0
Cyanoramphus ulietanus	Raiatea Parakeet	EX	Pacific	Raiatea, French Polynesia	−16.8	NA	0
Cyanoramphus zealandicus	Black-fronted Parakeet	EX	Pacific	Tahiti, French Polynesia	−17.7	NA	0
Eclectus infectus	Oceanic Parrot	EX	Pacific	Tonga	−18.7	NA	0
Nestor productus	Norfolk Kaka	EX	Pacific	Norfolk Island, Australia	−29.1	NA	0
Cyclopsitta coxeni	Coxen's Fig-parrot	CR	Australia	Eastern Australia	−26.2	93 600	<250
Lathamus discolor	Swift Parrot	CR	Australia	Eastern Australia	−31.8	21 500	1000–2500
Neophema chrysogaster	Orange-bellied Parrot	CR	Australia	Eastern Australia	−35.5	12 800	20–25
Cyanoramphus malherbi	Orange-fronted Parakeet	CR	New Zealand	New Zealand	−41.9	118 000	<250
Strigops habroptila	Kakapo	CR	New Zealand	New Zealand	−41.7	95 100	108
Charmosyna amabilis	Red-throated Lorikeet	CR	Pacific	Fiji	−17.2	37 100	<50
Charmosyna diadema	New Caledonian Lorikeet	CR	Pacific	New Caledonia	−21.4	1	<50
Cacatua sulphurea	Yellow-crested Cockatoo	CR	Wallacea	East Timor & Indonesia	−4.6	1 360 000	1500–7000
Charmosyna toxopei	Blue-fronted Lorikeet	CR	Wallacea	Buru, Indonesia	−3.4	9 100	<250

(564 000 km^2 ± 190 000 CI 95%, N = 158). On average, Extinct and Critically Endangered species were distributed at higher latitudes (23.8° S ± 6.4 CI 95%, N = 14) than less-threatened species (14° S ± 2 CI 95%, N = 158).

Large-bodied and island-inhabiting parrot species were found to be over-represented among extinct species at a global scale (Olah *et al.* 2016). Steadman (2006) reviewed the biogeography and extinction of parrots in Oceania, using archaeological evidence to record the prehistorical ranges of species, and reported at least 6 species that are now extinct in the tropical Pacific. Along with two *Cyanoramphus* and one *Eclectus* species, from French Polynesia and Tonga, respectively (Table 3), archaeological evidence suggests that one *Cacatua* species from New Caledonia and two *Vini* species from the Cook Islands also existed in the past (Steadman 2006). All four extinct *Cyanoramphus* and *Vini* species were larger than the closely related extant species, lending support to the finding that large-bodied parrot species are more prone to extinction (Olah *et al.* 2016). Biodiverse island ecosystems, such as those in Oceania, can accumulate many vulnerable and endemic species over time, which ultimately raises the extinction risk in this region (Weeks *et al.* 2016).

Priorities for research and conservation

The status of parrots is reassessed by BirdLife International every 4 years (most recently in 2016) using published information (e.g. Danielsen *et al.* 2010; Freeman *et al.* 2013; Freeman and Freeman 2014; Sam and Koane 2014), unpublished reports (e.g. Swinnerton and Maljkovic 2002), theses (e.g. Heptonstall 2010), and information provided directly by scientists, conservation practitioners and birdwatchers. However, assessing the status of poorly known species remains challenging. For example, the Red-throated Lorikeet (*Charmosyna amabilis*) may have been extirpated on some islands, but survey data remain insufficient to confirm its status (Watling 2013).

In Table 3 we list the threatened parrot species in Oceania that are particularly in need of conservation research and attention. Most of these species are now restricted to very small areas, mainly individual islands, which makes them highly vulnerable to invasive species and stochastic factors, such as extreme weather events. For certain species, 'insurance' populations in safe breeding facilities may be required as part of a wider recovery plan (Holdsworth and Starks 2006; Leus 2011; Collar and Butchart 2014). This pertains not only to Endangered and Critically Endangered species but also to those species that lack sufficient data to be assessed adequately. Even species that are categorised as Near Threatened may prove to be of significant conservation concern once further information is obtained on their distribution, population trends, and threats.

We identify hotspots for parrot diversity and conservation in Figure 3(A, B). These maps indicate that threatened parrots in the Pacific are scattered over many islands, yet New Caledonia stands out as a priority for conservation. Other important locations for parrot conservation are the South Island of New Zealand, the Australian island of Tasmania, and the Moluccas and Biak Island in Indonesia. Indonesia is undoubtedly a global priority for parrot conservation (Olah *et al.* 2016), and our results reinforce the need for conservation research across its vast archipelago. Although focused research and conservation initiatives are in place in New Caledonia, New Zealand, and Australia, similar programmes are lacking in Indonesia, and may be difficult to instigate due to restricted funding and access to certain locations. Nevertheless, we hope that the information provided here will draw attention to the threats facing parrots throughout Oceania, and foster support for the species and ecosystems most in need of protection.

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ORCID

George Olah http://orcid.org/0000-0002-7935-8843
Jörn Theuerkauf http://orcid.org/0000-0002-7273-3073
Andrew Legault http://orcid.org/0000-0002-4371-2302
Roman Gula http://orcid.org/0000-0002-0619-5123
Stuart Butchart http://orcid.org/0000-0002-1140-4049
Mark O'Brien http://orcid.org/0000-0002-0415-1602
Robert Heinsohn http://orcid.org/0000-0002-2514-9448

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